PHOSPHORUS AND PH TOLERANCES IN THE GERMINATION OF THE DESERT SHRUB *LARREA TRIDENTATA* (ZYGOPHYLLACEAE)

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ABSTRACT

Seeds of *Larrea tridentata*, a dominant shrub of deserts in the southwestern U.S., were germinated on both a pH and phosphorus (P) gradient to determine if requirements for germination can help explain the field distribution of *Larrea*. Germination decreased significantly above pH 8, which is consistent with the conspicuous absence of *Larrea* from high pH sodic or saline desert soils. Although *Larrea* tends to be absent from noncalcareous soil, seed germination was not inhibited in acidic solutions. Germination showed no response to P or to interactions of pH and P. In contrast, recent literature has suggested that *Larrea* may be restricted to calcareous soils of low phosphorus availability due to toxicity of high concentrations of P to seedlings.

Larrea tridentata (Sessé & Moc. ex DC.) Cov. (creosote bush) is one of the most abundant and widely distributed shrubs of southwestern deserts (Runyon 1934); its limits have been used to define the warm desert region of North America (Benson and Darrow 1954). Within its range, however, *Larrea*-dominated communities often exhibit sharp boundaries, and a complete transition to other communities may be seen within 5–10 meters (Barbour 1969). Age distributions of *Larrea* in mature communities and observations of germination in the field indicate that germination and survival of seedlings are rare events under natural conditions (Barbour 1969, Ackerman 1979, Boyd and Brum 1983, Goldberg and Turner 1986) and suggest that germination could affect the distribution of *Larrea*.

Several authors have shown that soils in areas dominated by *Larrea* are porous and have greater drainage and aeration than do soils of adjacent areas (Yang and Lowe 1956, Fosberg 1940, Lunt et al. 1973). Others have observed that *Larrea* is found on soils that are generally calcareous throughout the profile (Hallmark and Allen 1975, Gardner 1958). *Larrea* apparently has no unusual physiological demands for calcium (Ca) (El-Ghonemy et al. 1978), but soil $CaCO_3$ may modify physical and chemical soil properties that are essential to the survival of *Larrea* (Hallmark and Allen 1975, Johnson 1961).

One potential effect of free $CaCO_3$ in soil is the fixation of available phosphorus (P) onto carbonates. Chemical interactions between Ca and P have been well documented, both in experimental solutions and in natural systems (Griffin and Jurinak 1973, Avnimelech 1983,

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MADROÑO, Vol. 34, No. 1, pp. 63–68, 1987

Cole and Olsen 1959). Carbonates affect P levels in solutions through ion pairing with Ca, physical sorption, and the precipitation of calcium phosphate minerals (Marion and Babcock 1977). Fixation of P by soil carbonates may lower crop response to P fertilization in the southwest (McCaslin and Gledhill 1980, Chang 1953).

Musick (1978) found that P was toxic to *Larrea* seedlings at fairly low external concentrations (10 μM) in slightly acid solution cultures (pH 6). Because there was no toxicity response at pH 8, Musick suggested that *Larrea* is adapted to alkaline, calcareous soils of low P availability. In a study of the germination requirements and tolerances of *Larrea* seeds, Barbour (1968) found no differences in germination success in the pH range of 7–10. Barbour, however, used phosphate buffers of an unreported P concentration to establish these solution pH values. In the light of Musick's (1978) finding of a significant effect of P in seedling growth, we have reevaluated the germination tolerance of *Larrea* with respect to both pH and various levels of P.

Methods

Seeds of *Larrea tridentata* were collected in July 1984 from shrubs along a bajada of the Jornada Experimental Range of New Mexico State University near Las Cruces, New Mexico. Fruits from ca. 30 shrubs were mixed and stored in paper bags at room temperature until germination experiments began.

Experimental methods followed those of Barbour (1968), with several modifications. Whereas Barbour used whole mericarps in his germination trials, the high incidence of empty mericarps in our collections prohibited this technique. Mericarps were cracked open, and only mature seeds whose lengths were approximately 3 to 5 mm were used in the experiment.

Seeds were germinated along both a pH and a P gradient in a 2-way factorial design. The Modified Universal Buffer (MUB) of Skujins et al. (1963), a phosphate-free buffer used widely in phosphatase enzyme studies (Tabatabai and Bremner 1969), was used to establish the pH of the experimental solutions. Solutions of pH 7, 8, 9, and 10 were used as in Barbour (1968), as well as an additional treatment of pH 4.5. Buffers were mixed 1:1 with half-strength modified Hoagland's solution (Downs and Hellmers 1975) with a subsequent readjustment of pH. Treatment levels of P were 1) 1 μM, derived from the quarter-strength modified Hoagland's solution with no additional P added; 2) 10 μM; and 3) 100 μM PO_4-P, added as KH_2PO_4. These concentrations span the range of P levels used by Musick (1978).

In each treatment, we used 100 seeds grouped into 5 lots of 20 seeds each. As in Barbour (1968), seeds were soaked for 3 hours in

TABLE 1. NUMBER OF SEEDS THAT GERMINATED AFTER 5 AND 10 DAYS IN EACH pH × PHOSPHORUS TREATMENT. (abcde) values with the same letter within the pH × phosphorus factorial cross on each day are not significantly different by Duncan's multiple range test (5% level). (ABC) values with the same letter for pH treatments on each day are not significantly different by Duncan's multiple range test (5% level). * = one-way ANOVA indicates no significant differences (5% level) between values for phosphorus treatments on each day.

Day 5

	Phosphorus concentration			Mean over all phosphorus treatments
pH	1 μM	10 μM	100 μM	
4.5	12.0^{bc}	15.8^{a}	14.4^{ab}	14.1^{A}
7	13.4^{abc}	11.6^{bc}	12.0^{bc}	12.4^{A}
8	13.8^{abc}	10.2^{de}	16.2^{a}	13.4^{A}
9	13.0^{abc}	8.0^{de}	8.2^{de}	9.7^{B}
10	4.8^{e}	6.8^{de}	6.8^{de}	6.1^{C}
Mean over all pH treatments	11.4*	10.5*	11.5*	

Day 10

	Phosphorus concentration			Mean over all phosphorus treatments
pH	1 μM	10 μM	100 μM	
4.5	15.8^{ab}	17.4^{a}	16.6^{ab}	16.6^{A}
7	15.0^{abc}	16.2^{ab}	14.4^{abcd}	15.6^{A}
8	16.6^{ab}	13.2^{bcd}	17.0^{a}	15.2^{A}
9	14.4^{abcd}	11.8^{cde}	11.4^{de}	12.5^{B}
10	8.6^{e}	8.6^{e}	8.8^{e}	8.7^{C}
Mean over all pH treatments	14.1*	13.4*	13.6*	

the appropriate treatment solution, and each set of 20 seeds was transferred to a petri dish filled with sand moistened with the same solution. All dishes were incubated in darkness at 25°C. We tallied germinations after both 5 and 10 days, and observed no germination after this period.

Statistical analyses were performed using the ANOVA procedure of SAS (SAS Institute Inc. 1982). The number of seeds that germinated in each lot of 20 seeds was treated as one observation. When the ANOVA indicated statistical significance, Duncan's multiple range test was used to distinguish differences among treatments.

RESULTS

Although pH had a significant effect on germination ($p < 0.0001$), there was no effect of P concentration (Table 1). There were no

significant differences in germination among pH 4.5, 7, and 8, but the number of seeds that germinated declined sharply at pH 9 and 10. The ANOVA for day 5 counts showed a significant interaction between pH and P ($p < 0.0004$), possibly due to a high mean germination value for pH 9 (1 μM PO_4-P solutions) and a high value for pH 8 (100 μM solutions). The interaction was not significant on day 10, and we believe that it occurred as a result of random variation.

Discussion

Differences in methodology may account for the disparity between our results and those of Barbour (1968), who found no effect of pH on germination over the range of pH 7–10. Although his germination trials lasted 5 days, we found significant germination occurring between 5 and 10 days in seeds extracted from mericarps. Barbour (1968) found that root growth decreased greatly with increasing pH, especially above pH 8. The response curve of root growth to pH (Fig. 5 in Barbour 1968) is remarkably similar to the response of germination to pH found in this study. The lack of response of germination to P concentration probably reflects the high internal stores of P in seeds of *Larrea* (Barbour 1968, Musick 1978). Thus, nutrient absorption does not become significant until seedling emergence.

Our data show that relatively acid solution (pH 4.5) did not inhibit the germination of *Larrea* seeds. Barbour (1968) found that root growth was greater in slightly acidic solutions (pH 6) than in those of higher pH. Thus, germination and early root development in response to pH cannot be used to explain the distribution patterns of *Larrea* found by Hallmark and Allen (1975), who showed that shrubs were restricted to soils that were calcareous in the upper 10 cm.

Solutions of pH 9 to 10 frequently reduced germination to less than 50% of maximum, certainly an important reduction for a species that has no significant seed bank (Boyd and Brum 1983) and few years that are favorable for germination and establishment in the field (Ackerman 1978). This result is consistent with known *Larrea* distribution patterns. Calcic soils have pH's in the range of 8–8.4, and soil pH will be higher only when significantly sodic or saline. *Larrea* is conspicuously absent from saline soils near topographic lows and playas (Barbour 1969, Fosberg 1940, Went and Westergaard 1949).

Many of the environmental variables that appear to affect *Larrea* distributions are correlated, and thus it is difficult to discern cause-and-effect relationships in nature. Calcareous soils tend to have a well-buffered pH range and are often coarse-grained with good in-

ternal drainage, whereas soils of a higher pH tend to be saline and fine-grained, with a lower permeability. Lunt et al. (1973) showed that *Larrea* has a relatively high oxygen requirement for root growth, and the correlation between $CaCO_3$ and *Larrea* occurrence may be due to the improved aeration and root penetration in $CaCO_3$-rich soils rather than to the direct presence of $CaCO_3$ or to the buffering of soil pH by $CaCO_3$ (Lunt et al. 1973, Johnson 1961). Our data suggest that soil pH does not limit the germination of *Larrea* in acid, non-calcareous soils of southwestern deserts, although soil pH may interact with other factors to determine successful seedling establishment and growth.

Acknowledgments

This work was supported by a Sigma Xi Grant-in-Aid of Research to KL and NSF Grant BSR 8212466 to WHS. We thank Peter Vitousek, Brad Musick and anonymous reviewers for many helpful comments on the manuscript.

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(Received 10 Feb 1986; revision accepted 5 Aug 1986.)

ANNOUNCEMENT

New Publication

Rzedowski, J. and G. C. de Rzedowski (eds.), *Flora Fanerogámica del Valle de México,* Vol. 2, *Dicotyledoneae (Euphorbiaceae-Compositae),* Instituto de Ecologia, AP 18-845, Deleg. Miguel Hidalgo, CP 11800, México, D. F., 1985, 674 pp., illus., ISBN 968-7213-02-7, US $35.00 (hardbound). [The second volume of a proposed three-volume flora. Volume 1 (publ. Mar. 1979, reprinted 1984, 432 pp., US $28.00, source above) provided introductory information on topography, geology, climate, plant communities, etc., and a floristic treatment of gymnosperms and of dicotyledons from Saururaceae to Polygalaceae. Volume 3 will include the monocotyledons.]